

## Research Article

# The greater the proportion of *Robinia pseudoacacia* in a stand the greater its effect on the population characteristics of *Erythronium dens-canis*

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## Abstract

Management of invasive alien plants is an increasing problem throughout the world. In some cases native rare or protected species can appear or even prefer habitats dominated by invasive alien plants, which raises questions about the optimal treatment of such areas. *Erythronium dens-canis* in Hungary is a protected species which only have several occurrences in the country and a number of these populations situated in *Robinia pseudoacacia* stands developed after harvesting native forests. In this study a total of five populations of *E. dens-canis* were surveyed between 2020 and 2022 in southwestern Hungary examining and comparing the ongoing demographic changes under native and *Robinia* stands by monitoring individual plants. Two populations were situated in forests composed of native tree species, two in *Robinia pseudoacacia*-dominated stands and one in a *Robinia*-native tree species mixed stand. We categorized the plants into five age-state categories: dormant, seedling, juvenile, vegetative adult, and reproductive adult. We found some considerable differences (e.g. leaf size, reproduction rate) between the populations situated in native and in *Robinia* stands, whereas the population in mixed forest showed intermediate character in most examined factors. Based on our results, *R. pseudoacacia* have a significant effect on the phenology and life history of *E. dens-canis*, and this effect is greater with higher proportion of *R. pseudoacacia* in a forest stand where the *E. dens-canis* occurs.

**Key words:** Endangered species, habitat transformation, Hungary, invasive alien species, population dynamics



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## Introduction

One of the most problematic aspects of invasive alien plant species is their potential ability to transform ecosystems in which they are introduced to (Richardson and Rejmánek 2011). They can affect plant functional traits (Sitzia et al. 2018), influence community structure and composition (Daehler and Strong 1994; Hejda and Pyšek 2006; Gaertner et al. 2009; Nascimbene and Marini 2010) together with altering soil characteristics and nutrient cycling (De Marco et al. 2013; Medina-Villar et al. 2015). Biological invasions can lead to homogenization of native communities (McKinney and Lockwood 1999; Rooney et al.



2004), loss of biodiversity, including altered ecosystem functioning (Pimentel et al. 2001; Didham et al. 2007; Vilá et al. 2010).

In Hungary, *Robinia pseudoacacia* L. (black locust or false acacia) is one of the invasive alien plant species with the greatest impact on natural ecosystems (Mihály and Botta-Dukát 2006). *R. pseudoacacia* belongs to the legume family (Fabaceae), it is a light-demanding pioneer species native to North America. In its native range it rapidly colonises forest gaps and is gradually replaced by other tree species after 15–30 years. In contrast, in secondary habitats its populations can persist for longer periods, displacing native communities (Cierjacks et al. 2013) and therefore *R. pseudoacacia* is considered an invasive species throughout Europe, which resulted in the inclusion of this species in national blacklists and other lists summarising alien species (Norway: Gederaas et al. 2012; Czech Republic: Pyšek et al. 2012; Pergl et al. 2016; Germany: Seitz and Nehring 2013; Italy: Celesti-Grappo et al. 2009; Switzerland: FOEN 2010).

It was one of the first American tree species to be introduced to Europe in the early 17<sup>th</sup> century (Vadas 1914; Vítková et al. 2016) due to its numerous economically positive properties (Vadas 1914; Göhre 1952; Straker et al. 2015). Since then, *R. pseudoacacia* has played a major role in forest management in Hungary, resulting in a significantly higher proportion of black locust forests than in other Central European countries (Vítková et al. 2017). The share of *R. pseudoacacia* in the managed forested areas is the highest (nearly 460 thousand hectares, about 24%; KSH 2023) of all tree species, and its area is still increasing (KSH 2023).

Several authors have shown that the herbaceous level of *R. pseudoacacia*-dominated forests differs significantly from that of native forests in Europe (Wendelberger 1954; Montagnini et al. 1991; Peloquin and Hiebert 1999; Von Holle et al. 2006; Taniguchi et al. 2007; Vítková et al. 2016). Under the canopy of *R. pseudoacacia*, conditions are more favourable for shade-tolerant and nitrophilous species (Hruška 1991; Cierjacks et al. 2013; Vítková et al. 2016).

In the first half of the growing season, two different phenological aspects of the herb layer are observed in *R. pseudoacacia*-dominated forests (Vítková et al. 2017). In early spring, before the appearance of *Robinia* leaves (March–April) geophytes and ephemeral annuals are observed. In late spring (May–June), shade-tolerant annuals, common nutrient-demanding plants and grasses appear. In the second half of the growing season, annuals and geophytes disappear and the herb layer often dries out (Vítková et al. 2017).

As agricultural intensification in Europe resulted in substantial loss of natural habitats (Tilman et al. 2001), there has been a gradual selection towards species that can survive in secondary habitats or on the edge of cultivated fields, especially when the management is extensive (Perrino et al. 2014). This process, although in a slower pace, is still in progress, and therefore the conservational value of semi-natural habitats is gradually increasing, as for example for annual meadows of the *Thero-Brachypodietea*, that give refuge to some rare and endangered plant species (Brana et al. 2014; Perrino et al. 2022, 2023), and are considered a priority habitat of the Directive 92/43/EEC. In Hungary, several rare and endangered species occur in *Robinia*-dominated stands, such as *Erythronium dens-canis* L., *Crocus reticulatus* Steven ex Adams or *Sternbergia colchiciflora* Waldst. Et Kit. (Bagi et al. 1998; Pacsai et al. 2022). As *E. dens-canis* only has a few large populations in Hungary and a number of these are situated in



*Robinia* forests, the better understanding of the species biology and ecology in this specific situation is essential to plan suitable treatments of these habitats. Relatively little is known about the population biology of *Erythronium* species in general, a few long-term studies have been carried out so far with *E. japonicum* Decne. (Kawano et al. 1982) and *E. americanum* Ker Gawl. (Holland 1981), and two study concentrated on *E. dens-canis*, one in Italy (Pupillo and Astuti 2017), and one in Ukraine (Kricsfalusy et al. 1995) where the detailed morphological and demographic properties of multiple populations were monitored through five years.

In our study we started a long-term monitoring of five *E. dens-canis* populations occurring in forests with different compositions: natural forests consisting of native tree species, intermediate, mixed and semi-natural, *Robinia*-dominated stands to follow the demographic and structural changes taking place in each population. During the first year of the study we noticed considerable differences in phenology and demography of the *E. dens-canis* plants in native and in *Robinia* stands (significantly different-sized individuals in same age-states, different ratio of flowering and pollination), which prompted us to expand our study with more, intermediate type sites to investigate these differences between populations situated in these two types of habitats in more detail.

## Materials and methods

### The dog's tooth violet (*Erythronium dens-canis* L.)

*E. dens-canis* is a monocotyledonous, perennial geophyte species, belonging to the lily family (Liliaceae). Mature specimens of the species are 10–30 cm tall (Király 2009). It flowers before trees leafing out, starting in mid-February. The vegetative plants produce one leaf, reproductive ones produce two leaves, varying in shape from ovate to lanceolate, slightly fleshy, ashy green, with brown spots that fade by the end of the growing season (Király 2009; La Rocca et al. 2014). It produces its characteristic, pink (rarely white) flowers with recurved petals with dark purple (rarely yellow) stamens, usually solitary, on 8–25 cm peduncles. The fruit is a tricarpic capsule, in which the seeds ripen in May. The seeds have an elaiosome, which is dispersed by ant species (myrmecochoria) (Gutián et al. 2003). It occurs in dry to mesophilic, usually slightly acidic soils, in hornbeam-oak woodlands, beech woodlands, mountain meadows, less frequently in wet meadows, but mainly in older, more open forest stands (Király 2009, Vacek et al. 2020).

All members of the genus *Erythronium* are native to the northern temperate zone. In Europe, only one of them, *E. dens-canis* is native. In Asia, three more species [*E. caucasicum* Woronow, *E. sibiricum* (Fisch. & C.A.Mey.) Krylov and *E. japonicum* Decne.] are present, and 23 species occur in North America (Kawano 2005). Despite the fact that *E. dens-canis* is listed as a threatened species in several European countries [Hungary: near threatened (Király 2007), Austria: regionally endangered (Niklfeld and Schratt-Ehrendorfer 1999), Slovakia: vulnerable (Turis et al. 2014), Romania: vulnerable (Hurdu et al. 2022)] or only small local populations occur [Czech Republic (Vacek et al. 2020), Ukraine (Tykhonenko et al. 2017), Hungary (Nagy et al. 2019)], few studies have investigated the life history, ecology and population dynamics of the species (Kricsfalusy



and Mihaly 1993; Kricsfalusy et al. 1995; Guitián et al. 1999; Mondoni et al. 2012; Pupillo and Astuti 2017).

Similar studies have been carried out mainly on species occurring in America (*E. americanum*, *E. grandiflorum* Pursh) and Japan (*E. japonicum*) (Holland 1974; Muller and Bormann 1976; Yokoi 1976; Kawano et al. 1978; Holland 1980; Kawano et al. 1982; Hughes 1992; Ruhren and Dudash 1996; Sawada et al. 1997; Takada et al. 1998; Kawano 2005; Tessier 2019). As these species have similar life histories, they are occurring in similar habitats and genetically close to *E. dens-canis* (especially *E. japonicum*, which some authors describe as a subspecies of *E. dens-canis*), we used literature related to these species as well in the design and preparation of the present research.

Study area and permanent plots

In 2020 we installed permanent quadrats (1×1 m) along transects at three locations (one near Becsehely and two near Lispeszentadorján villages) for long-term monitoring of *E. dens-canis* populations. The corners of these quadrats were marked with nails and numbered aluminium plates to ensure the accurate positioning of the 1×1 m frames (with 10 cm wire grids) which helped us in repeated locating of individuals. Two of the studied *Erythronium* populations situated in native forest stands (Native 1, Native 2: Lispeszentadorján 1 and 2; abbreviations: N1, N2) and one in a *R. pseudoacacia*-dominated, secondary forest (*Robinia* stand 1: Becsehely 1; abbreviation: R1). In 2021 two more set of permanent quadrats have been installed, one in a *Robinia*-dominated stand (*Robinia* stand 2: Becsehely 2; abbreviation: R2) whose population was discovered in 2020, and one in a stand composed of approximately half *Robinia* and half native tree species (Native-*Robinia* mix: Lispeszentadorján 3; abbreviation: NR) (Table 1). In each area, we installed enough quadrats (their number varied between 7 and 16 per site) to have included at least 100 individuals per sample area. The positions of each *Erythronium* individual within the quadrats were recorded by 1 cm accuracy and they were marked individually by nails equipped with numbered aluminium plates. This way we were able to find the same individuals repeatedly throughout the years.

Since it is very difficult to determine precisely the age of some bulbous species, demographic-population dynamics studies often classify individuals into age-state categories based on various physical parameters (Rabotnov 1985). In our study, we used methods commonly used for population dynamics studies of geophyte species and age-state classification based on leaf morphology

Table 1. Description of the sample sites.

Sample sites and their abbreviations in parentheses	dominant tree species	locality (WGS84, DD; X,Y)	elevation (m a.s.l.)	no. of censused plants between 2020 and 2022 (min–max)
Lispeszentadorján 1 (N1)	<i>Quercus robur</i> , <i>Carpinus betulus</i>	46.52987°N, 16.70998°E	225	110–185
Lispeszentadorján 2 (N2)	<i>Fagus sylvatica</i> , <i>C. Betulus</i>	46.53225°N, 16.71440°E	220	146–172
Lispeszentadorj 3 (NR)	<i>Robinia pseudoacacia</i> , <i>C. Betulus</i> , <i>Q. Robur</i>	46.52972°N, 16.71071°E	230	80–104
Becsehely 1 (R1)	<i>R. pseudoacacia</i>	46.46072°N, 16.79269°E	210	112–294
Becsehely 2 (R2)	<i>R. pseudoacacia</i> , <i>C. Betulus</i>	46.46271°N, 16.78128°E	245	276–396



measurements, which have been proven suitable for other *Erythronium* species (Yokoi 1976; Kawano et al. 1982; Sawada et al. 1997) as we assessed this method in our earlier study on *E. dens-canis* (Pacsai et al. 2022). We measured maximum length (without petiole) and width of each leaf of every individual (besides seedlings, as their length were recorded only), and presence or absence of reproductive organs at the end of the flowering period (April) between 2020 and 2022.

## Data analysis

Leaf area was estimated using a coefficient derived from proportions of leaf areas to leaf length and width ratio measured by image analysis of 76 leaves of 56 *E. dens-canis* individuals, photographed in 2020 at the study sites (Pacsai et al. 2022).

One of the main difficulties in the case of perennial species is the separation of juvenile individuals and vegetative adults. As we wanted to study the long-term life history of individuals of this species and it is also protected by law in Hungary, we used only non-destructive methods during the data collection. Therefore we couldn't examine the bulbs of the individuals which otherwise could have provide significant help in categorizing the plants into age-states (Kricsfalussy et al. 1995). We used leaf area of the smallest (but statistically not outlier) reproductive individuals as the boundary line between the juvenile and vegetative adult age-state categories. As the time of measurement and environmental factors affect plant growth, this limit should be estimated for each year and each site separately (Jeong et al. 2022; Pacsai et al. 2022).

Since it cannot be determined whether a plant is dead or dormant at this point (the possible length of the prolonged dormant period is not yet known), we considered dead only seedlings which did not appear in the following years. Beside these instances, we categorized the plants as dormant when they did not produce aboveground organs. Calculating population growth ( $\lambda$ ) without including mortality rates obviously results in skewed values, but it still makes it possible to compare each population with some certain limitations.

Numerical analyses (descriptive statistics and one-way ANOVA with post-hoc Tukey-tests) were carried out using IBM SPSS 22.0 and R version 4.1 (R Core Team 2015). The figures presented in this paper were prepared with R and ggplot2 package (version 3.4.2). Calculation of deterministic growth rates ( $\lambda$ ) was done in R with package popbio (version 2.7, Stubben and Milligan 2007).

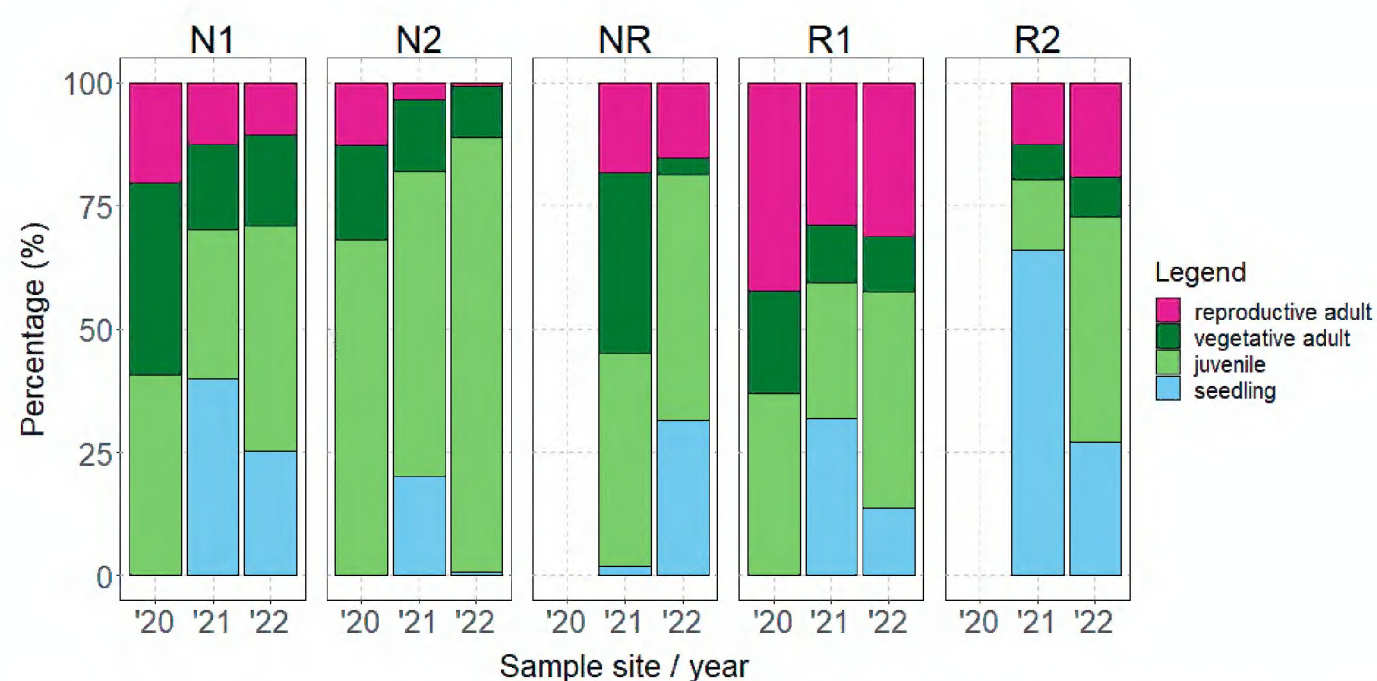
## Results

The number of individuals present at a sample site showed notable changes between years (Table 1), which is partly due to individuals which did not appear aboveground in some years (we found such plants in all sites and in all years after the baseline survey), but more influenced by the high fluctuations in the number of seedlings each year. In 2020 there were no seedlings present in the surveyed quadrats, we found only a very few around the sample sites. In contrast, at most sites, in 2021 a high number of seedlings appeared which was followed by a lower, but still considerable amount in 2022. Only the NR site showed a different trend, where the number of seedlings was higher in 2022 (Fig. 1).





**Figure 1.** Population structure at each sample site between 2020 and 2022, seedlings included.



**Figure 2.** Population structure at each sample site between 2020 and 2022 with the exclusion of seedlings.

With the highly fluctuating seedlings category omitted, the population structure at each sample site during the three years show some uniform trends (Fig. 2). The fraction of juvenile individuals gradually increased at all sample sites during the study years. This was mainly caused by the substantial increase in the number of juvenile individuals, but in the case of N1, N2 and NR the decrease in the numbers of vegetative and reproductive adult individuals also contributed to this rearrangement in population structure. At sites with *Robinia pseudoacacia* dominance (R1, R2) the proportion of reproductive adults in the population and the ratio of vegetative/reproductive adults were notably higher than at sites with native tree species (N1, N2) for each year. The population structure of *E. dens-canis* population in native-*Robinia* mix stands (NR) was similar to native sites (N1, N2) in 2021, while in 2022 it was close to *Robinia* dominated sites (R1, R2).

Although seedling lengths were quite similar in 2021 and 2022 at each sample site (Fig. 3), we found significant differences between different sites in both years. Sites separated into two groups by statistical analyses (one-way variance analysis followed by Tukey-tests), with the R1 and R2 sites together with



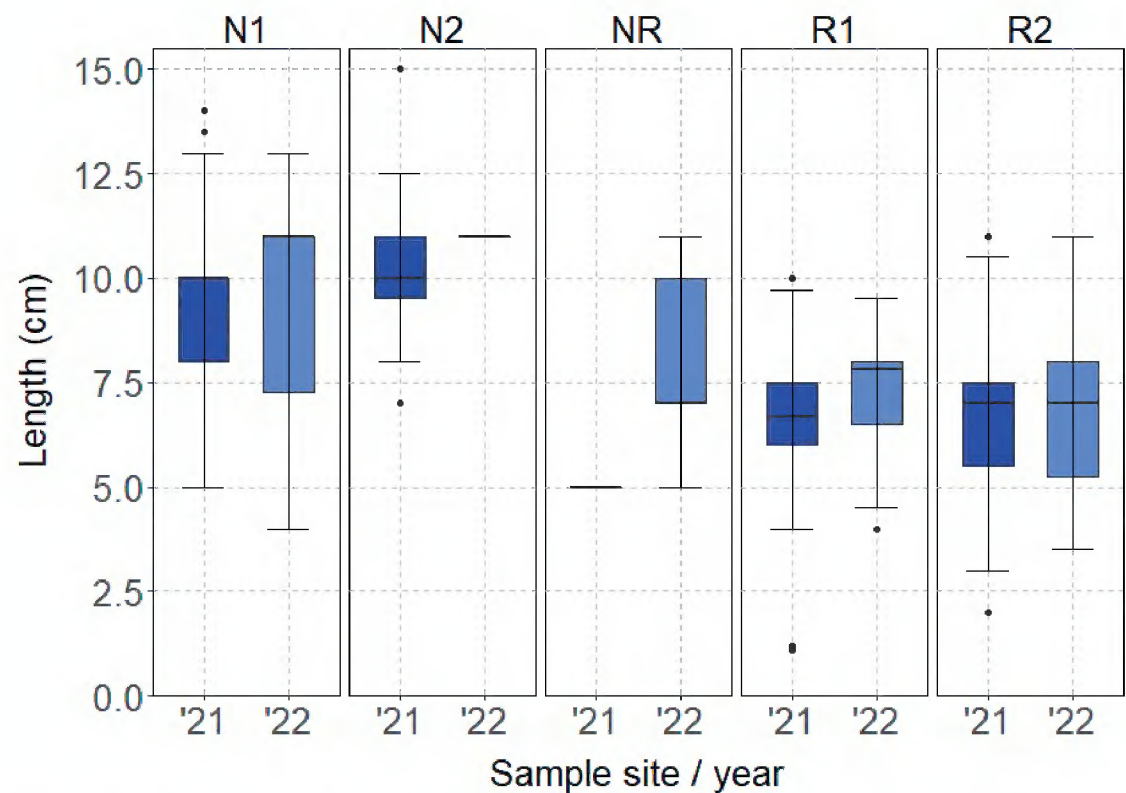


Figure 3. Length of seedlings at each sample site between 2021 and 2022.

Table 2. Number of cases (N) and means of vegetative characteristics of different age-states at the five sample sites between 2020 and 2022. The grouping results of ANOVA followed by Tukey tests is indicated in uppercase.

	Year	N1		N2		NR		R1		R2	
		N	Mean	N	Mean	N	Mean	N	Mean	N	Mean
Seedling length (cm)	2020	0	–	0	–	n.a.	n.a.	0	–	n.a.	n.a.
	2021	74	93.74 <sup>b</sup>	35	98.86 <sup>b</sup>	2	50.00 <sup>a</sup>	63	66.83 <sup>a</sup>	266	66.47 <sup>a</sup>
	2022	26	96.35 <sup>b</sup>	0	–	27	79.82 <sup>a</sup>	28	71.29 <sup>a</sup>	99	70.95 <sup>a</sup>
Juveniles leaf area (cm <sup>2</sup> )	2020	40	6.17 <sup>a</sup>	75	6.10 <sup>a</sup>	n.a.	n.a.	36	15.45 <sup>b</sup>	n.a.	n.a.
	2021	56	6.50 <sup>ab</sup>	107	4.95 <sup>a</sup>	45	6.42 <sup>ab</sup>	60	8.72 <sup>b</sup>	57	6.81 <sup>ab</sup>
	2022	48	2.50 <sup>a</sup>	128	3.06 <sup>a</sup>	43	6.23 <sup>b</sup>	89	4.13 <sup>a</sup>	167	2.43 <sup>a</sup>
Vegetative adult leaf area (cm <sup>2</sup> )	2020	38	28.10 <sup>a</sup>	21	27.50 <sup>a</sup>	n.a.	n.a.	20	60.69 <sup>b</sup>	n.a.	n.a.
	2021	32	34.39 <sup>b</sup>	25	25.13 <sup>a</sup>	38	35.33 <sup>b</sup>	17	48.85 <sup>c</sup>	29	47.56 <sup>c</sup>
	2022	19	17.70 <sup>a</sup>	15	26.78 <sup>ab</sup>	3	46.95 <sup>c</sup>	23	39.14 <sup>bc</sup>	29	34.27 <sup>bc</sup>
Reproductive adult leaf area (cm <sup>2</sup> )	2020	19	44.92 <sup>a</sup>	9	35.44 <sup>a</sup>	n.a.	n.a.	37	60.82 <sup>b</sup>	n.a.	n.a.
	2021	22	43.46 <sup>ab</sup>	5	29.39 <sup>a</sup>	19	51.69 <sup>bc</sup>	56	52.74 <sup>bc</sup>	50	71.33 <sup>c</sup>
	2022	8	28.63 <sup>a</sup>	0	–	3	55.48 <sup>ab</sup>	58	58.01 <sup>b</sup>	64	68.53 <sup>b</sup>

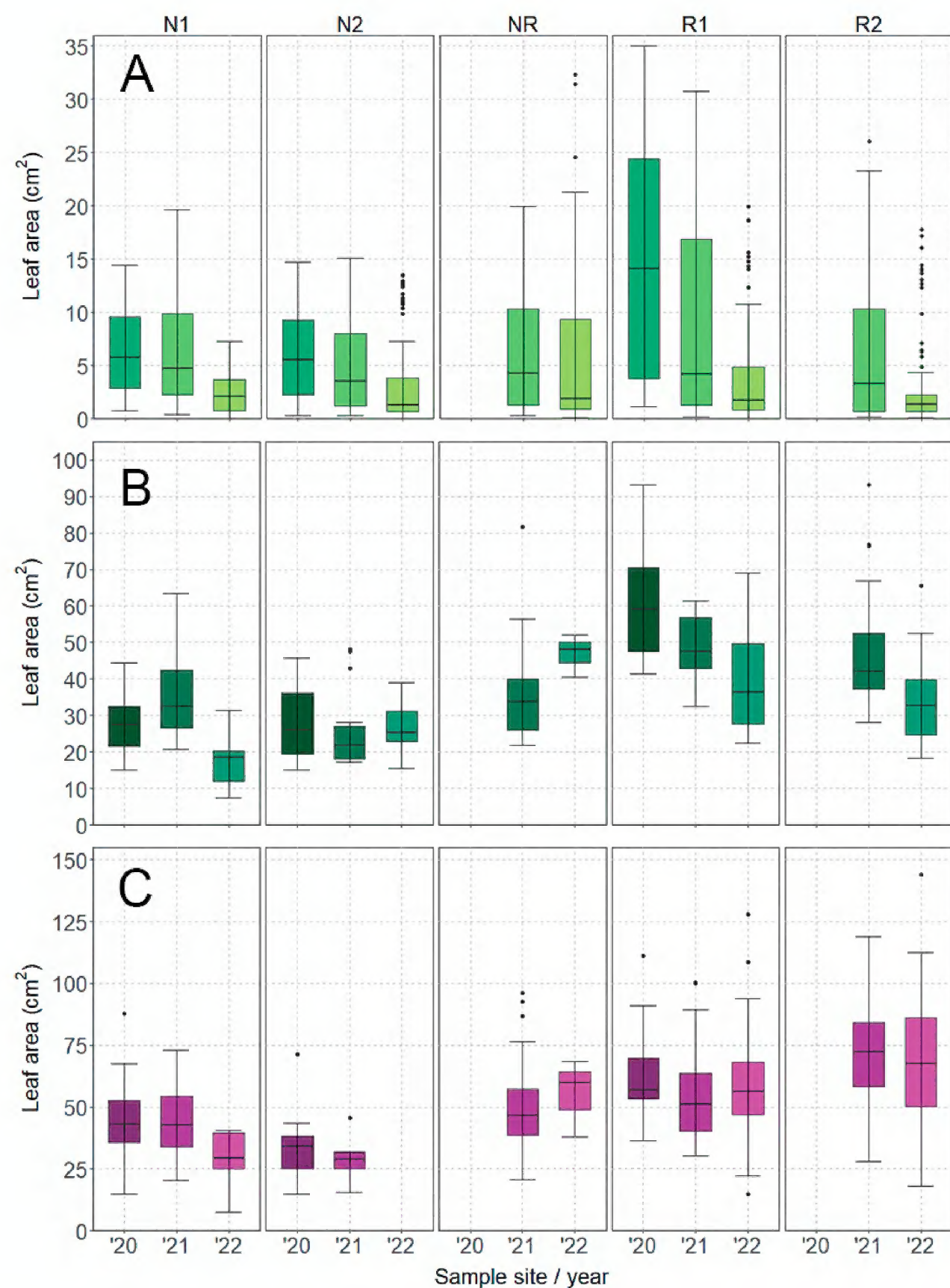
NR forming one ( $p = 0.201$  in 2021 and  $0.177$  in 2022) and N1 and N2 sites forming the other in 2021 ( $p = 0.966$ ). In 2022 the latter group consisted of only N1 since the absence of seedlings at N2 in that year (Table 2).

Leaf areas of juvenile plants showed a similar decreasing trend in all sample sites during the three years (Fig. 4), most remarkably in R1. Although in 2021 and 2022 there were marked differences between the maximums of leaf areas, their means were much closer to each other (Table 2).

In the case of adult individuals (both vegetative and reproductive), their leaf areas were the largest at R1 and R2 sites, followed by NR, while the two sites with natural habitats had the smallest leaves in all three years. The extent of these differences varied between years (Table 2).

In all three sample sites which were surveyed over the three years, in 2022 we found adult individuals (10 vegetative and 2 reproductive) which were not





**Figure 4.** Leaf area of juvenile (A), vegetative adult (B) and reproductive adult (C) individuals at each sample site between 2020 and 2022.

recorded before, which suggests that *E. dens-canis* could become dormant for at least two years. Transition matrices also reveal that all age-states are prone to dormancy (Suppl. material 1). At sites with *Robinia*, reproductive plants had much higher tendency to flower again in subsequent years (32–86%) and juvenile plants developed into vegetative adult category in higher percentage. In terms of recruitment we did not observe notable trends as the rate of recruitment at each site varied greatly in some cases. The overall growth rates ( $\lambda$ ) of the populations also show some differences between sites (Table 3). During the first transition (2020–21) the one site with *Robinia* cover (R1) had the lowest growth rate by far (0.792) of the three surveyed sites, the two populations situated in native forest stands (N1, N2) had a  $\lambda$  close to 1 which is a characteristic of stable populations. However, during the 2021–2022 transition, this trend reversed, the two populations under *Robinia* (R1, R2) had the highest growth rate, while the ones under native stands (N1 and N2) had the lowest (still close to 1) and the mixed stand (NR) had a  $\lambda$  between the values of these two groups.



Table 3. Projected population growth rates ( $\lambda$ ) of each site.

Sample site	2020–2021	2021–2022
Native 1 (N1)	0.929	1.046
Native 2 (N2)	0.978	1.001
Native-Robinia mix (NR)	–	1.067
Robinia 1 (R1)	0.792	1.128
Robinia 2 (R2)	–	1.365

Discussion

Between 2020 and 2022 the number of individuals surveyed in the quadrats at sites with native tree species were more constant than at sites with *R. pseudoacacia*. These differences were mainly caused by the more pronounced recruitment in some years at the latter sites. Besides this difference in most sites the gradual increasing proportion of juvenile individuals in the populations was observed. Comparing the demographic characteristics of the studied populations with literature data we found that at the N1 and N2 site the demography of the *Erythronium* populations is very similar to what Kricsfalusy et al. (1995) described as “left-sided”, which means the dominance of young individuals, the highly dynamic seedling category and marginal proportion of adult plants in the populations. The populations situated in mixed forests showed somewhat similar trends, but with the growing proportion of *Robinia* in the forest stands (NR, R2, R1) the demographic distributions of the *Erythronium* populations gradually changing towards the “right-handed” state described by Kricsfalusy et al. (1995) with the difference that the seedling category is also significant and highly fluctuating. Despite the fact that prolonged dormancy (not producing aboveground shoots during one or more growing seasons even though the plant is still alive) has been reported in several genera of the lily family (Tyler and Borchert 2002; Delvallée et al. 1990; Miller et al. 2004; Tatarenko 2019), we found no mention in the literature about the observation of this phenomenon regarding any species of the genus *Erythronium*. We found only mention of ‘senescent’ plants by Kricsfalusy et al. (1995) as old, dying bulbs without leaves. In contrast, at all sites in both years after the baseline survey we found individuals from multiple age-states which were not present aboveground in the previous one or two years. The relatively high number of such plants indicates that this phenomenon is most likely not only the result of occasional damage occurring to plants, but a natural characteristic of the species.

The average size of adult individuals was significantly greater in the populations under *Robinia* than at the sites in native forests in all three years. Such a difference would hardly be explained by the location, exposure or geology of the sample sites, and it is therefore assumed that differences in the composition of the forest stands in the sample sites may be the cause of this phenomenon. It is known that *R. pseudoacacia* can significantly increase the amount of nitrogen available for uptake by *Rhizobium* bacteria (Rice et al. 2004), often resulting in a significant increase in the leaf area of species in its understory (Guo et al. 2021).

Although the mean of leaf areas of juvenile plants decreased in all areas throughout the three years, the lower limit of the leaf area of reproductive



individuals did not change as much. Thus, even smaller plants became adults in each following year, which could be the result of gradual environmental changes or just a coincidence in weather patterns.

One transition does not tell much about recruitment or growth rate of the population (Crawley 1990), as these values are highly variable, likely depending on environmental factors among others as well. However, it is notable that although the  $\lambda$  value of the one population under *Robinia* (R1) during the 2020–21 transition was the lowest among all sites, in the next transition the  $\lambda$  values of *Robinia* stands were the highest by far. The populations situated in native stands had a similar growth rate (close to 1) in both transitions. As in 2020 we could not find any seedlings in any surveyed quadrats, and in 2021 and 2022 there were numerous in some sites, these great differences in recruitment rates likely caused by annual variances in weather. Great differences between recruitment rate at different sites have been observed in the case of this species (Kricsfalussy et al. 1987) but in our study these contrasts cannot be attributed to differences in geographical conditions as all our study sites are situated in the same landscape and the NR site which is just 50 metres in distance from the N1 site shows the highest similarities with the R2 site (9 km away). The low  $\lambda$  value of R1 in the 2020–21 transition means that the population without recruitment is rapidly declining even with the mortality rates omitted during the calculation of deterministic growth rates. In the 2021–22 transition the presence of recruitment made  $\lambda$  considerably higher than the 2020–21 value, which suggests that in *Robinia*-dominated habitat type *E. dens-canis* is highly relying on recruitment and these populations could be characterized by a more dynamic demography which is generally uncommon in long-lived herbaceous species (Eriksson 1989), but not unknown for *E. dens-canis* (Kricsfalussy et al. 1995).

In contrast with the R1 and R2 populations, the *E. dens-canis* populations situated in native forests have more stable demographical characteristics, their growth rate was close to 1 with or without recruitment. The *Robinia*-native tree species mixed stand (NR) showed an intermediate growth rate, which also suggests that the greater the ratio of *Robinia* in a stand the greater is its effect on the *Erythronium* population as well. Since these values were also calculated without the mortality rates of most age-states, the growth rates are likely lower. It could easily change the growth rate of populations in native forest stands from stable or slowly growing to a declining category.

## Conclusions

Nitrogen pollution originating from agricultural activities (fertilization, production of leguminous crops) is a common potential threat to biodiversity, especially to endangered species (Hernández et al. 2016). The habitat-transforming capability of *R. pseudoacacia* is already known, which is mostly caused by increasing nitrogen input into the ecosystem (Buzhdygan et al. 2016; Vítková et al. 2016), however its effect on endangered plant species is a less studied topic. Our results agree with previous studies (Buzhdygan et al. 2016) that *R. pseudoacacia* accelerates environmental processes, as *E. dens-canis* populations under *R. pseudoacacia* show much more volatile deterministic growth rates and higher turnover compared with populations situated under native tree



species and this effect was greater in sites with greater ratio of *Robinia* in the tree cover. Such variations in the life cycle of plants may support the dynamic heterogeneity of populations which in turn ensures their stability in different environmental conditions and management regimes (Kricsfalussy 2016). In most aspects, where we found differences among populations, the extent of these differences was in correlation with the proportion of *R. pseudoacacia* in the forest stands, as the population at the NR site often showed intermediate characteristics between the native and *Robinia*-dominated stands.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

Conceptualization: JB, BP. Data curation: VL, BP, EAB. Formal analysis: BP. Funding acquisition: JB. Investigation: BF, EAB, BP, VL. Methodology: JB. Project administration: JB. Resources: EAB. Supervision: JB. Validation: VL, BF. Visualization: BP. Writing – original draft: BP, JB. Writing – review and editing: JB, BP.

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### Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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## Supplementary material 1

### Transition matrices of *Erythronium dens-canis* populations between 2020 and 2022

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Data type: docx

Explanation note: Transition matrices of *Erythronium dens-canis* populations in five sample sites (2 in native forests, 2 in *Robinia pseudoacacia*-dominated stands and 1 in mixed, native-*Robinia* stands) in Hungary between 2020 and 2022.

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